

carried through the winter for seed production. Elimination of such sources of virus usually gives a high degree of control. The spread of X-disease on peach can be prevented by removing all infected chokecherries within 500 feet of peach orchards, and the virus diseases of raspberries can be controlled, in most instances, by destroying all wild and escaped brambles in the immediate vicinity of plantings, provided the plantings themselves are not already infected.

Reducing the population of insect vectors by spraying or by other means has value in the control of some virus diseases. Usually it is not possible, however, to reduce the insect populations sufficiently or soon enough to obtain completely satisfactory results. Some virus diseases can be partly controlled by destruction of the hosts of the insect vectors. Extensive reduction of the weed hosts of the beet leafhopper in the Western States would correspondingly reduce the amount of curly top virus carried from desert plants to cultivated fields. In much of this area, reduction in weed hosts comes about naturally under systems of land management in which annual and perennial grasses and other nonhost plants are allowed to replace the weed hosts of the beet leafhopper. Fall spraying to kill leafhoppers on weeds in uncultivated areas has been resorted to also in the program to control curly top.

Virus-free nursery stock is extremely important in the control of virus diseases of strawberry and raspberry. Natural virus spread often is not extensive enough to cause serious damage during the life of plantings started with virus-free nursery stock. That is true also of some of the virus diseases of tree fruits.

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How Insects Transmit Viruses

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Most viruses that cause plant disease are transmitted by insects, principally those that have sucking mouth parts—aphids, leafhoppers, white flies, mealybugs, and tingids. Leafhoppers and aphids are the most important.

Although many plant viruses are without known insect vectors, it is generally expected that insect carriers will eventually be discovered for most of them. There are exceptions. Tobacco mosaic virus and potato latent virus are two viruses that occur in high concentration in infected plants and are stable enough to be spread readily from one plant to another by almost any means that releases juice from a wound in an infected plant and transfers the juice to a fresh wound in a healthy plant. Tobacco mosaic virus is thus transferred by the hands of men working with tobacco plants even though the wounds may be only microscopic in size. It can also be thus transferred by the mouth parts of grasshoppers. Potato latent virus can be transferred from plant to plant when the wind blows the leaves of diseased plants against healthy ones so as to injure both. The mystery about these two viruses is not their transmission by such methods but why potato latent virus is apparently not transmitted by sucking insects and why tobacco mosaic virus is so poorly transmitted.

A few viruses, such as wheat rosette virus and lettuce big-vein virus, contaminate the soil in which diseased

plants are grown and infect healthy plants subsequently grown therein. Just how inoculation takes place in such diseases is not known. Dodders (*Cuscuta* species), parasitic flowering plants, can transmit plant viruses by means of the natural graft unions they make with their hosts. Most plant viruses, however, depend on insects for their dispersal.

APHIDS transmit more plant viruses than any other group. Aphid-borne viruses induce in plants a great variety of symptoms, the most important of which are the mosaics. One of the most efficient aphid vectors is the green peach aphid, *Myzus persicae*, which transmits more than 50 different plant viruses.

Much remains to be learned about what actually occurs during transmission by aphids. Many aphid vectors transmit virus after very brief feedings on diseased plants. Studies on this type of transmission have reached a point where the feeding intervals of individual aphids are closely observed and timed by a stop watch. For example, the vector of beet mosaic virus requires an acquisition feeding of only 6 to 10 seconds. During subsequent consecutive inoculation feedings of 10 seconds each on healthy plants, the virus is gradually lost by the aphids and fewer than 2 percent of them can transmit to more than four plants without fresh access to virus. This virus is said to be nonpersistent in the vector. Usually such a virus is lost more rapidly from feeding aphids than from fasting ones—the virus of cucumber mosaic disease, for instance, is lost by the aphid within 6 to 8 hours when fasting, but within 10 to 20 minutes when feeding on healthy plants. In other instances this relation may be reversed. The loss of virus from aphids during feeding may be due to a virus-inactivating enzyme secreted by the aphids while feeding but not while fasting. Such a substance has not been demonstrated, however, and in reality we do not know the explanation for

such loss and for many other features of aphid transmission. A virus transmitted by aphids, particularly if it is of this nonpersistent type, is usually transmissible by several or, indeed, many species. The virus of onion yellow dwarf can be transmitted by more than 50 species of aphids, but not by thrips, mites, grasshoppers, beetles, caterpillars, or maggots.

That kind of transmission is in contrast to another type in which, following acquisition of virus, a latent period must elapse before the aphid is able to transmit. The aphid may then do so for many days without fresh access to virus. A minority of viruses transmitted by aphids are spread in that manner. One of them, the virus of potato leaf roll, is not transmitted by the aphid until 24 to 48 hours have elapsed after acquisition. The virus may then be retained by the insect for 7 to 10 days, even through molts, without fresh access to virus from plants.

That an aphid may transmit one virus in the persistent manner and another in the nonpersistent from the same host plant clearly indicates that persistence or nonpersistence is determined by the virus.

Why do we concern ourselves with such minute details of transmission? Simply because such knowledge may make the difference between success and failure in finding a vector of a virus. For instance, no transmission of a certain mosaic virus could be obtained after extensive trials with three species of aphids when they were fed one day on diseased plants and then transferred to healthy ones. When the aphids were fasted for 30 minutes before an acquisition feeding of 5 to 10 minutes and were then allowed an inoculation feeding of 5 to 10 minutes, however, transmissions were obtained.

LEAFHOPPERS, next to aphids, are the most important vectors of plant viruses. Experiments by a Japanese grower in 1884 demonstrated a connection between rice stunt and leafhoppers. That might be considered

the first virus shown to be insect-transmitted, but actually it was not realized until more than 20 years later that the causal agent of the disease was not the leafhopper but some autonomous agent carried by the insect.

Viruses transmitted by leafhoppers cause a variety of symptoms in plants, including chlorotic streaking of leaves (as in corn streak), necrosis or death of tissues (as in elm phloem necrosis), tumors (as in wound-tumor disease), and yellows (as in aster yellows). All known vectors for virus diseases with a symptom picture like that of aster yellows are leafhoppers.

Although many aphid-borne viruses can be transmitted by rubbing leaves with juice from diseased plants, only two leafhopper-borne viruses have been so transferred. In other cases transmission has been accomplished only by the use of insects, dodder, or grafting. This has accordingly made the study of the viruses themselves very difficult. For such researches it has been necessary to permit the leafhoppers to feed on virus solutions through membranes or to inject the virus solution into leafhoppers. The insects must then be tested for infectivity on plants because none of the leafhoppers themselves has ever been observed to be diseased.

Practically all of the leafhopper-borne viruses (alfalfa dwarf virus is apparently an exception) are considered to have a latent or incubation period in their vectors. In some, this latent period may be so short (curly top virus) as to suggest that the virus does not multiply in the insect. Nevertheless, it reaches relatively high concentrations and is retained for weeks, not only in the beet leafhopper, which transmits it, but also in a number of other arthropods that cannot do so.

In most leafhopper vectors that have been studied, however, the period that occurs between acquisition of the virus and its transmissibility by the vector is much longer. In many it varies from 1 to 2 weeks or more. This is a true incubation period, during which the

viruses multiply to an infective concentration in their vectors.

Although most leafhopper vectors do not transmit virus to their progeny through the egg, certain exceptions exist. Rice stunt virus and clover club leaf virus may be passed to 95 or 100 percent of young insects through the eggs of the vectors. A single female leafhopper carrying clover club leaf virus has originated at least 21 generations of infective progeny during a 5-year period without fresh access to virus from plants. The virus in the original female had been diluted at least 100,000,000,000,000,000,000,000,000,000,000,000,000,000,000 times. That would be impossible had not the virus multiplied in the leafhopper.

There may be, then, two main types of transmission of virus by leafhoppers. One type, exemplified by curly top virus, may be characterized by a very short incubation period and no multiplication in the vector; the other type by a long period of incubation and multiplication in the vector.

Once infective, leafhoppers tend to remain so for many days without fresh access to virus, often until they die. Nevertheless, such insects may fail to infect susceptible plants for many days in succession. Some that obtain virus from their parent through the egg may in turn pass virus to their progeny through the egg and yet may fail to infect any susceptible plants although fed on them for their entire life.

Often scientists have tested so many species of insects before finding a leafhopper vector that when they attained success they regarded the vector as specific. Only one species is known even today to transmit North American curly top virus. Very likely that is because it is the only species of the genus that occurs in North America where tests have been made.

The concept of specificity which envisioned a single leafhopper species as the vector of a virus has been broken down by recent research. For example, it is now known that Pierce's disease of grapes is transmitted by 24 different

species of leafhoppers in two families. On the other hand, work with yellow dwarf and with curly top viruses has revealed a new type of specificity, of considerable complexity. In the former, there are two varieties of virus, each specifically transmitted by related leafhoppers. In the case of curly top, we have evidence of a complex of related viruses, with different vector and plant-host relationships.

Much of the wide variation observed in vector efficiencies of individuals within a leafhopper species may be genetic. For example, ability to transmit corn streak virus can be determined by a single sex-linked dominant gene in the insect vector. In the case of the leafhopper that carries New York potato yellow dwarf, multiple factors are involved, the virus having been transmitted by 80 percent of the "active" insects, 2 percent of the "inactives," and 30 percent of hybrids.

Considerable experimental work has been done on various aspects of the transmission process by the leafhopper. The mechanics of the mouth parts, the tissues of the plants reached by the mouth parts, and the location of the virus within the insect vector have all been subjects of investigation. Most leafhoppers apparently acquire virus from and introduce virus into the phloem. However, some vectors feed on the xylem and acquire virus from and inoculate it into this tissue. Some viruses show a corresponding specialization in regard to the tissues they attack.

WHITE FLIES transmit a number of plant viruses. Nymphs of the white fly are attached to the plant and therefore cannot themselves spread virus, but virus can be acquired by the nymphs, can pass through the pupal stage, and can be transmitted by the adults. The adults also can acquire the virus directly from plants.

When white flies were shown in 1946 to be vectors of a virus of abutilon, a puzzle of long standing was partly solved. Variegated abutilon had been

used as an ornamental for many years in Europe and other parts of the world where the variegation never spread naturally to nonvariegated plants.

Since there was no natural spread of the condition, the disease was sometimes set somewhat apart from other virus diseases even though the variegation could be transmitted by grafting. It is now evident that in some countries a virus causing a similar variegation is disseminated in the field by a white fly.

MEALYBUGS, tended and transported by ants, are the vectors of destructive viruses that attack cocoa trees. Some of the viruses are closely related; in other cases relationships are uncertain. The viruses, which are not transmissible to plants by juice inoculations, do not remain long in the mealybugs unless they fast before the acquisition feeding; then virus may be retained about 36 hours. In spite of the nonpersistence of the virus, there is some specificity of transmission—certain mealybug species transmit certain of the virus strains not transmitted by others, and vice versa. Moreover, some strains of one of the mealybug species failed to transmit a virus that other strains of the same species transmitted.

THE ONLY VIRUS definitely known to be transmitted by thrips is the one that causes tomato spotted wilt. Forty-one different plant viruses have been tested for transmission by thrips with negative results. Although three species of thrips are vectors of tomato spotted wilt, several other thrips species are not. Tomato spotted wilt virus can be acquired only by larvae, but it passes through the pupal stage, so that both adults and larvae can inoculate plants. After an incubation period of 5 days or more the insects remain infective for life.

We have relatively few authenticated accounts of transmission by insects with biting mouth parts. In some of these isolated cases, there is better transmission of the virus by biting insects than by those with sucking

mouth parts. The virus of turnip yellow mosaic is an example of this kind of virus. It apparently is not transmissible by insects with sucking mouth parts but is transmitted by a number of insects with biting mouth parts. The most important of these are flea beetles, the larvae of which may retain virus for as long as 4 days. It is believed that the insects regurgitate the virus.

All viruses of this sort are readily transmitted by rubbing juice from diseased plants on the leaves of healthy ones, and some are readily isolated.

UNTIL RECENTLY the only viruses photographed under the electron microscope were the more stable ones, which are readily transmitted mechanically and occur in relatively high concentration in plants. Some are insect-transmitted. Among them are the tobacco mosaic and squash mosaic viruses. Less stable and less concentrated viruses that have a more intimate relationship with their vectors have been identified recently under the electron microscope. Considerable interest attaches to the nature of those viruses that are known to reproduce in both plants and animals.

When one considers that the occurrence of a virus disease of plants usually involves three entities—the virus, the plant, and the vector—and may involve more than one of each, it should at once be apparent that the interactions between them and their environment may be exceedingly complex. In the laboratory, certain single factors may be demonstrated to be decisively important. Thus the virus of aster yellows is inactivated at 89° F. But when one tries to explain the vagaries of the spread of virus diseases in the field, relationships are not always readily discerned. For example: Northern regions and high altitudes with climates inimicable to aphids generally favor the production of potatoes with a low virus content, but hot and dry climates are also unfavorable for aphids and under certain conditions can be used to produce seed

potatoes with a low incidence of virus.

The flight habits of aphids in the field in relation to the spread of potato virus diseases have been extensively studied at Rothamsted in England and the Maine Agricultural Experiment Station. It was determined in Maine that early and sustained flights containing a high proportion of *Myzus persicae*, an aphid vector of leaf roll disease of potatoes, were associated with considerable spread of the disease. But flights late in August or in September usually resulted in little or no spread.

Detailed work has been done on the ecology of the vector of the curly top virus. This leafhopper is an active flier, and large numbers can easily be borne long distances by the wind. It often multiplies in the spring on a variety of succulent weeds on uncultivated or abandoned lands. If those plants dry up after the insects have reached the winged adult stage, the insects take flight. One such migratory flight was estimated at 60 miles. Forecasts of leafhopper invasions based on studies of the breeding areas have been used to reduce losses.

In general the insect vectors of a virus tend to be confined to one of the major phylogenetic divisions, such as the families of the Hemiptera or the order Thysanoptera. Some of the viruses multiply in their insect carriers and more may be expected to be placed in this category. The vector relationships of such viruses are obviously quite different from those of the viruses that do not multiply in the vector. Although more extensive research on certain viruses has greatly increased the number of known vectors for each, other research has at the same time indicated more highly specific virus-vector relationships than were indicated in early work.

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